Habitat Suitability and Herbivore Dynamics

by

Stavros Busenberg
and
Jorge X. Velasco-Hernandez

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Stavros Busenberg* Jorge X. Velasco-Hernandez†

Abstract

We derive a dynamic model for a plant herbivore system describing the interaction of a gall forming aphid and a single plant. We compare the behaviour of our model with experimental observations obtained from an aphid plant system studied by Whitham (1978). A simple parameter estimation shows a close correlation between the predicted and observed results.

1 Introduction

One of the important plant characteristics that determines the dynamics of a plant herbivore interaction is the suitability of the plant as habitat for the herbivore population. Habitat suitability denotes a very complex set of physiological and environmental conditions that provide minimum requirements for herbivore survival and reproduction (Soberon, 1986), and it constitutes the principal factor subjected to intraspecific competition in herbivorous insects.

Plant suitability can be measured in different ways depending on the particular kind of herbivore. Nevertheless, it is possible to distinguish intrinsic

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†Mathematics Department Claremont Graduate School, Claremont CA. 91711. Partially supported by CONACYT

plant components such as available nitrogen, secondary components, water content (Soberon, 1986), leaf size (Whitham, 1978), toughness, and micronutrient content (Schult, 1983), that affect the feeding behaviour, growth rate, and reproduction of herbivores(Kareiva, 1986). Other factors exist affecting the physiological or even physical status of a plant and that indirectly influence herbivore fitness. In this paper we consider a single individual plant whose foliage is viewed as composed of different groups, each one with a certain 'quality' with respect to the herbivore population, the high quality groups being the ones that provide the best habitat for survival and reproduction. In this way, leaf quality is a variable that aggregates a very diverse collection of physico-chemical factors of individual patches (individual leaves or groups of leaves) from which habitat suitability can be estimated. This approach to modelling herbivore plant relations based on plant quality was first developed by Edelstein-Keshet(1986). In her work she observed changes of plant quality through time as related to changes in herbivore density on plants and vice versa. Later on we will come back to this author and will expand our comments regarding our somewhat different modelling approach.

Herbivores of different kinds relate in different ways to their host plant. There is nothing that could possibly be called the general herbivore and, for this reason, one has to work with special cases. This work is concerned with herbivores of limited mobility. Their interactions with their host are restricted to a single individual plant on which they can disperse. As in Edelstein Keshet (1986), the plant trait subject to competition is plant quality. Our aim here is to give a simple model which takes into account the above considerations and also fits the available experimental data.

We make the assumption that the mortality rates of herbivore populations can be separated into two components: one reflecting the effect of resource quality on survival and reproduction, and the other representing density dependent regulation, i.e., the result of intraspecific competition.

We avoid the use of equations of the Lotka Volterra type for our model, since the dynamics of prey predator systems are very different from those of herbivory (Crawley, 1983). First, herbivores affect the birth rate of plants (Crawley, 1983) by eating seeds or reproductive organs, but do not directly affect their death rate. In normal situations they produce non-lethal damage to the plant. On the other hand, plants have a very strong influence on the herbivore death rate because of the limited variety and amount of food, shelter, or nesting sites that one species is able to use for its survival (Crawley,

1983). Hence, there is a habitat limiting factor to the growth of the animal population as a whole. The scarcer the habitats suitable for the herbivore, the greater the number of animals that die. As a result, there can be fluctuations in the abundance of the herbivore populations and yet, the plant abundance can remain fairly constant. What can vary in plants is not their total number but some other feature related to the suitability of the plant material as habitat for the herbivores. This is the feature that we call leaf quality.

Another factor which we do not consider here is that plant responses to infestation can depend on the infestation history. This means that the previous infestation levels influence the current one (McCrea and Abrahamson, 1987). This fact can produce an interesting delay effect in the plant herbivore interaction.

The responses of the herbivore to changes in plant quality which we consider are restricted to the possibility for an insect to change its foraging site within the individual plant, for example going from one leaf to another which is, possibly, of different quality.

In the next section we derive a mathematical model for such a herbivore system. In the third section we give the analysis of the model and use it to produce leaf qualities and insect population distributions. In the fourth section we compare the predicted results with the data for the gall forming aphid *Pemphigus betae* that has been studied by Whitham (1978).

2 Modelling habitat quality and herbivore dynamics

We consider a herbivore population living (feeding, nesting, reproducing, etc.) on the leaves of an individual plant whose foliage is divided into different quality classes. The leaf classes have different physico-chemical properties affecting survival probability, and the herbivores compete for the quality that provides the highest individual fitness. In our general model for this type of insect-plant interactions, we focus our attention on the behaviour of gall forming aphids.

We begin by dividing the components of herbivory into two broad classes: herbivore dynamics and plant dynamics. The leaf population is also assumed to be divided into two subpopulations: those leaves with no herbivores and

those leaves with at least one herbivore living on them. Thus we define

$n(q,t)$=*frequency of colonized leaves in the plant whose quality is* q *at time* t

and, hence, $\int_q^{q+\Delta q} n(q,t)dq$ is the number of invaded leaves on the plant whose quality falls within the range $(q, q+\Delta q)$.

$b(q,t)$=*frequency of bugs living on leaves of quality* q *at time* t

and $\int_q^{q+\Delta q} b(q,t)dq$ is the number of bugs living on leaves whose quality falls within $(q, q+\Delta q)$. Also, let

$$N(t) = \int_0^1 n(q,t)dq, \quad B(t) = \int_0^1 b(q,t)dq; \tag{1}$$

represent the total invaded leaf population and the total herbivore population living on leaves of all qualities respectively. We normalize the quality variable so that $q = 1$ denotes leaves of maximum quality. Invaded leaves are identified with leaves in which at least one gall has been formed.

2.1 Model assumptions

Let $\Delta t > 0$ and $\Delta q > 0$ be small increments of time and quality respectively. Given that $\Delta t < 1$, and assuming that the variation of quality with time satisfies $\frac{\Delta q}{\Delta t} = -\nu_1(q)$, and that there are no mortality nor migratory processes in the interval $(t-\Delta t, t)$, then

$$b(q,t) = b(q+\nu_1(q)\Delta t, t-\Delta t,).$$

Note that we are assuming that leaves get older with time and that this process is reflected in lower quality for older leaves. All newborn leaves are of maximum quality ($q = 1$). The above expression then says that the frequency of galls formed on leaves of quality q at time t is the same as was present at time $t-\Delta t$, when those same leaves were younger; i.e., of quality $q+\Delta q = q+\nu_1(q)\Delta t$. Thus, expanding the right hand side in Taylor series, and letting $\Delta t \to 0$, one obtains

$$\frac{\partial b}{\partial t} = \frac{\partial b}{\partial q}\nu_1(q). \tag{*}$$

The derivation for the leaf dynamics follows an analogous reasoning and hence will be omitted. We present now the assumptions under which recruitment, and removal rates and boundary conditions are to be added to the model.

(i) First we treat the removal rates of both the leaf and insect populations. For the herbivore population it is assumed that the removal of bugs from leaves of a given quality is only dependent on the quality of the leaves and on the total density of the population. There is no effect of the leaf population as such. This removal rate includes both mortality and emigration factors; that is, there are removed individuals that reappear in leaves of different qualities after leaving some other leaf in the same individual plant.

(ii) As for the leaf population, it is assummed that the removal rate of leaves is independent of the density of bugs settled already at any given time. However, it is assumed quality dependent, and also dependent on the total leaf load of the plant. In conclusion we are assumming an hervibore independent removal rate for the leaf population.

(iii) The assumptions on the 'recruitment' rates of both populations are as follows: For the herbivore population, the boundary condition will represent the colonization process of leaves of quality one by the herbivore. It is not representing a birth process. In fact we assumme that bugs on leaves of quality different from one, tend to migrate to leaves of quality one.

(iv) The corresponding rate for the leaf population is indeed a birth process. We state the mechanism by which leaves of quality one are produced in the plant. Now, in the biological situation that we model, there exist two possibilities with regard to the abandonment of leaves. Either a bug leaves the leaf and goes searching for another or the bug attempts a colonization and is unsuccesful that is, it dies. Both processes can provide 'new' aphid-free leaves that may be suitable for colonization. These leaves are assumed of quality less that one. We assume in this model that the proportion of aphid-free leaves is directly proportional to the density of colonized leaves, and also that the proportion of uncolonized leaves at any given time is much larger than the proportion of already colonized leaves.

Let $r(q,B)$ be the probability that all individuals on a leaf of quality q, when the total herbivore load in the foliage is B, have an unsuccesful colonization. Then

$$U(t,B) = \int_0^1 r(q,B)b(q,t)dq$$

is the total number of aborted galls at time t. Assume that the number of these leaves that are reinvaded successfully is proportional to the number of leaves of that quality and to a function, β, of the number of free aphids. Assume also that

a) The velocities $\nu_i = 1$, for $i = 0, 1$.

b) The number, $B_o(t)$, of free aphids is constant.

c) The removal rates for the gall and the invaded leaf populations are constructed with the assumptions (i) and (ii) above and are further asummed to be separable (Busenberg and Iannelli, 1985):

$$\mu_0(q,N) = \mu_0^{(1)}(q) + \mu_0^{(2)}(N),\ \mu_1(q,B) = \mu_1^{(1)}(q) + \mu_1^{(2)}(B).$$

Our model equations are

$$\frac{\partial n}{\partial t} - \frac{\partial n}{\partial q} = -\mu_0(q,N)n + U(t,B)\beta_2(B_o)(q,t), \tag{2}$$

$$\frac{\partial b}{\partial t} - \frac{\partial b}{\partial q} = -\mu_1(q,B)b. \tag{3}$$

The above equations, can be expected, in general, to have a quality, and perhaps also density dependent 'velocity' term as coefficient of the rate of change with respect to quality in equation (*). In this model we are assuming the velocity term to be constant and, by rescaling time we obtain equations (2) and (3).

Remark: As previously noted, Edelstein-Keshet(1986) constructed a set of models in which quality is the plant attribute that is involved in the interaction with the herbivore population. The relevant models to the one presented in this paper have the form

$$\frac{\partial b}{\partial t} + \frac{\partial bf}{\partial q} = 0$$

where f depends both on q and b, although in her case, quality increases with time and the nature of this variable is analogous to that of age or size. On the other hand, by defining $b(q,t)$ as the density of insects per leaf of quality q at time t, we restrict the 'velocity' terms that could appear multipying $\partial b(q,t)/\partial q$, to depend only on the quality or to be constant. This allows us to construct an independent equation for b without having to worry about the appearance of 'shock waves' that could arose if the velocity term mentioned above would depend also on b. By contrast, Edelstein-Keshet considered the more realistic setting described above, in which the velocity term depends both on quality and on b. But then b is viewed as independent variable and she studies the dynamics of $p(q,b,t)$ defined as the frequency distribution of plants of quality q and herbivore load b at time t. It should be mentioned that Edelstein-Keshet(1986) develops a whole set of different models applicable to several different forms and processes involved in herbivore plant interactions.

Returning to our model, for the boundary conditions, assume that once an individual reaches a leaf either it stays on it, or tries to move to one of maximum quality. Let $u_1(q)$ be the probability with which an insect on a leaf of quality q, moves to some leaf of quality 1 and succesfully colonizes it.

With these assumptions, $b(1,t)$ represents the total number of insects alive on leaves of quality 1 coming from leaves of all other qualities, and is given by

$$b(1,t) = \int_0^1 u_1(q)b(q,t)dq. \tag{4}$$

For the leaf population, let $m := \int_0^1 qn(q,t)$ be the mean invaded leaf quality of the plant; let R be the maximal potential density of leaves of quality 1 when no insects are present; let $V(B(t))$ represent the insect leaf use index as, for example in Soberon (1986), with $0 \leq V \leq 1$. Hence, $n(1,t)$ is the density of leaves of maximum quality at any time, and is given by

$$n(1,t) = Rm(1 - V(B)).$$

Rewrite the above relation as $n(1,t) = \int_0^1 u_0(q,B)n(q,t)dq$ where $u_0(q,B) = Rq(1 - V(B))$. Finally, at $q = 0$ no bugs can survive and leaves are permanently part of the uncolonized pool of leaves, respectively. Hence, the boundary conditions are given by (4) and

$$n(1,t) = \int_0^1 u_0(q,B)n(q,t)dq, \tag{5}$$

with the biologically appropriate assumptions

$$\lim_{q\to 0} n(q,t) = 0, \text{ and } \lim_{q\to 0} b(q,t) = 0. \tag{6}$$

The initial distributions of bugs and leaves are given by

$$n(q,0) = \varphi_0(q), \text{ and } b(q,0) = \varphi_1(q); \tag{7}$$

with ϕ_o and ϕ_1, given non-negative functions. Equations (2) to (5) constitute the model that we analyze in this work.

Remark: Note that condition (6) restricts the space of functions that will be considered as possible solutions.

3 Asymptotic behaviour of the model.

The plant-herbivore model obtained at the end of the previous section is solved by taking advantage of the separability property of the mortality functions of both herbivore and leaf populations, following the method developed by Busenberg and Iannelli (1985). We give a brief sketch of the technique as applied to our herbivory model. For more details we refer the reader to the paper cited above.

Define the ratios

$$\omega_0(q,t) := \frac{n(q,t)}{N(t)}, \quad \omega_1(q,t) := \frac{b(q,t)}{B(t)};$$

which represent the *quality profiles* of the leaf and herbivore populations; i.e., the proportion of these populations belonging to each quality class. It is easy to see that the following equations are satisfied by the quality profiles, given that n and b satisfy equations (2) to (5).

$$\frac{\partial\omega_0}{\partial t} - \frac{\partial\omega_0}{\partial q} + \mu_0^{(1)}(q)\omega_0 = -\omega_0 \int_0^1 [u_0(q,B) - \mu_0^{(1)}(q)]\omega_0 dq, \tag{8}$$

$$\frac{\partial\omega_1}{\partial t} - \frac{\partial\omega_1}{\partial q} + \mu_1^{(1)}(q)\omega_1 = -\omega_1 \int_0^1 [u_1(q) - \mu_1^{(1)}(q)]\omega_1 dq. \tag{9}$$

Also,

$$\frac{dN}{dt} = (\int_0^1 [u_0(q,B) - \mu_0^{(1)}(q)]\omega_0 dq - \mu_0^{(2)}(N) + BF(\omega_1,B))N, \tag{10}$$

$$\frac{dB}{dt} = (\int_0^1 [u_1(q) - \mu_1^{(1)}(q)]\omega_1 dq - \mu_1^{(2)}(B))B, \tag{11}$$

where $F(\omega_1, B) := \int_0^1 \beta(B_o) r(q, B) \omega_1(q,t) dq$.

The initial and boundary conditions are

$$\omega_i(q,0) = \Phi_i(q) \ , \ \lim_{q \to 0} \omega_i(q,t) = 0 \text{ for } i = 0,1;$$

$$\omega_0(1,t) = \int_0^1 u_0(q,B)\omega_0(q,t)dq \ , \omega_1(1,t) = \int_0^1 u_1(q)\omega_1(q,t)dq,$$

with $\Phi_0(q) = \varphi_0(q)/N$ and $\Phi_1(q) = \varphi_1(q)/B$, and ω_i satisfying

$$\int_0^1 \omega_i(q,t)dq = 1, \ i = 0,1.$$

Observe now that, if we can solve equation (9) for ω_1, then it is possible to solve equation (11) for B by substituting the solution for ω_1 in it. Next, with the solutions for B and ω_1 in hand, one can solve first, equation (8) for ω_0, and then the solution of equation (10) can be completely determined.

Note that the ordinary differential equations for the total leaf and herbivore populations are, in general, nonautonomous. However, because of the asymptotic properties of the solutions ω_0 and ω_1, one can study the asymptotic autonomous ordinary differential equations for B and N. This technique relies heavily on the properties of the solutions to the partial differential equations (8) and (9). For this reason, we describe the method of solution of equation (9).

We assume that u_1 and $\mu_1^{(1)}$ are non-negative functions on $[0,1]$; u_1 is bounded, and $\int_0^\epsilon \mu_1^{(1)}(q)dq = \infty$ for any $\epsilon > 0$. This last requirement simply means that herbivores cannot survive by living on plant tissues of zero quality. In the same way, we require a similar property for the quality-dependent mortality of leaves, since old leaves with very low quality certainly die. In order to guarrantee these conditions, we assume that $\int_0^1 \mu_i^{(1)}(q)dq = \infty$, and $\mu_i^{(1)}(q) \geq 0, \ i = 1,2$, approaches infinity as q approaches zero. Define

$$\Pi_1(q) := exp(-\int_q^1 \mu_1^{(1)}(r)dr). \tag{12}$$

This is the probability that an herbivore, originally living on a leaf of quality 1, will survive when the quality deteriorates to q, $q < 1$.
Similarly,

$$\Pi_0(q) := exp(-\int_q^1 \mu_0^{(1)}(r)dr), \tag{13}$$

is the probability that a leaf of quality 1 still be functional when quality deteriorates to q, $q < 1$. The biological fact that animals living on leaves of zero quality eventually die is expressed by the property

$$\Pi_1(0) = \lim_{q \to 0} exp(-\int_q^1 \mu_1^{(1)}(s)ds) = 0. \tag{14}$$

Equations of the type we are dealing with can be shown to have a unique solution whose asymptotic behaviour depends on the real solutions $\lambda = p_1^*$ of the equation

$$\int_0^1 exp(-\lambda(1-q))u_1(q)\Pi_1(q)dq = 1, \tag{15}$$

and such that

$$\int_0^1 exp(-p_1^*(1-q))\Pi_1(q)dq < \infty.$$

The nonlinear renewal theorem of Busenberg and Iannelli (1985) implies that ω_1 satisfies

$$\lim_{t \to \infty} \omega_1(q,t) = \omega_1^\infty(q) = \frac{e^{-p_1^*(1-q)}\Pi_1(q)}{\int_0^1 e^{-p_1^*(1-q)}\Pi_1(q)dq}.$$

The following important relation which involves the first term of the right hand side of equation (15) also holds,

$$\lim_{t \to \infty} \int_0^1 [u_1(q) - \mu_1^{(1)}(q)]\omega_1(q,t)dq = p_1^*.$$

As has been already observed, we can now apply this last result in equation (11) obtaining, as time goes to infinity, the limiting equation

$$\frac{dB}{dt} = (p_1^* - \mu_1^{(2)}(B))B. \tag{16}$$

If we assume that $\mu_1^{(2)}(B)$ is a non-negative monotone increasing function with $\mu_1^{(2)}(0) = 0$, then $B(t) \to B^*$, a constant, as $t \to \infty$. By the eventually non-decreasing nature of $\mu_1^{(2)}$, all solutions are bounded and reach an asymptoticaly stable equilibrium point. The non-trivial case, p_1^* positive, provides us with the asymptotic solution of the equation for the herbivore population:

$$b(q)^\infty = \frac{e^{-p_1^*(1-q)}\Pi_1(q)B^*}{\int_0^1 e^{-p_1^*(1-q)}\Pi_1(q)dq}. \tag{17}$$

Knowing ω_1 and B, the next step consists in solving the equations for the leaf population. From the definition of $u_0(q, B)$, and since B asymptotically reaches a stable constant equilibrium value, then $u_0(q, B)$ tends to a limit $\psi(q)$ which does not depend on the insect density as time goes to infinity. We can now apply the same procedure we used with equation (12). First, we find the persistent solutions and the number $\lambda = p_0^*$; with these we can find the expression for the asymptotic behavior of ω_0 which is given by

$$\omega_0^\infty(q) = \frac{e^{-p_0^*(1-q)}\Pi_0(q)}{\int_0^1 e^{-p_0^*(1-q)}\Pi_0(q)dq}.$$

If $h(q) = r(q, B^*)$ is a bounded integrable function, then

$$\lim_{t\to\infty} \int_0^1 \beta r(q, B)\omega_1(q, t)dq = \int_0^1 \beta h(q)\omega_1^\infty(q)dq = k_{B^*}.$$

Here k_{B^*} is a constant which combined with

$$\lim_{t\to\infty} \int_0^1 [\psi(q) - \mu_0^{(1)}(q)]\omega_0(q, t)dq = p_0^*;$$

yields the asymptotic autonomous ordinary differential equation for N, and the asymptotic solution for n :

$$\frac{dN}{dt} = (p_0^* - \mu_0^{(2)}(N) + k_{B^*}B^*)N \tag{18}$$

$$n(q)^\infty = \frac{e^{-p_0^*(1-q)}\Pi_0(q)N^*}{\int_0^1 e^{-p_0^*(1-q)}\Pi_0(q)dq}, \tag{19}$$

where N^* is the limiting value of $N(t)$. In order to get the existence of a unique limit N^*, we are assuming that $\mu_0^{(2)}$ satisfies the same hypothesis as $\mu_1^{(2)}$.

Equations (17) and (19) are explicit expressions for the densities of the herbivore and leaf populations. These are the results we shall use in comparing the predictions of this model with experimental data.

4 Fitting observed data and conclusions

The experimental results obtained by Whitham (1978) were used to test the model. Whitham studied mechanisms of habitat selection in response

to resource limitations and competition of a population of the leaf-galling aphid *Pemphigus betae*. This aphid lives on leaves of *Populus angustifolia*, on which fertile individuals develop with colonization success depending on the eventual size of mature leaves. Experiments showed that, as leaf size at maturity increased, the percentage of stem mothers that died declined, and further results indicated that aphids selected large leaves for colonization (Whitham, 1983). The quality of the leaves was measured by leaf size.

Leaf size, however, is correlated with other factors that are more adequate for our modelling purposes. Whitham (1978) indicates that large leaves are more suitable habitats because the amount of nutrients needed by *Pemphigus* is correlated with leaf size. This correlation is important for our model since we are assuming that leaf quality decrease with time and with the action of the aphids upon the leaf. Leaf size does not decreases with time in the case of aphid herbivory, although the functional photosynthetic area, for example, does. Hence, we use the association of leaf size and quality, taking it as an indirect measure of photosynthetic area or concentration of nutrients.

Density dependence, which enters the removal rates in the model, was another factor evaluated in this experiment. In the absence of competition, the reproductive output of *Pemphigus* is limited by the quality of leaves and, as this factor becomes more important, stem mothers are forced to colonize smaller leaves since larger ones are scarce. Density is measured as the number of galls in leaves, which is equivalent to the number of stem mothers. Predation is not an important regulating factor in this interaction (Whitham,1978).

We now proceed to fit the theoretical distribution provided by the model to the field data obtained by Whitham. This author provided us with the experimental quality distributions for *Pemphigus* and for the leaf population. This information is displayed in Table 1. Recall that in our model leaves are born with quality 1 and that leaf quality decreases with time. Also, recall that for the aphid population the 'birth' term at $q = 1$ represents an emmigration process in which all aphids colonize leaves of maximum quality, with a probability that depends on the mean quality of the leaf in which they are settled.

Leaf size, used by Whitham as a quality measure, was standarized by dividing it by the maximum size, which was taken to be equal to 17.5 cm^2, obtaining in this way, a quality index varying on the interval $[0, 1]$. However, quality classes used by Whitham were discrete. For the comparisons we

make here, we have subdivided the interval [0,1] into seven subintervals and we have taken the middle point of each as our coresponding quality index value. For the fitting of equations (17) and (19) to the data points, the Levenberg-Marquardt procedure was applied to estimate μ_i and p_i^*. For both populations, the quality dependent mortality was assumed to be of the form

$$\mu_i^{(1)}(q) = q^{-1} + \mu_i(1-q) \text{ for } i = 0, 1. \tag{20}$$

The term q^{-1} guarantees the satisfaction of the mathematical restriction $\Pi_i(0) = 0$ in equations (12) and (13).

The fit shown in Table 1 and graphically in Figures 1 and 2, is reasonable good, if one considers the relatively few sample points provided and the number of parameters adjusted. The value of $p_0^* < 0$ gives a unimodal distribution. On the other hand, the herbivore quality distribution is also a result of a quality dependent outflow rate given by equation (20). In this case $p_1^* > 0$ produces a nondecreasing insect distribution with quality.

To interpret the parameters p_0^* and p_1^* we go back for a moment to equations (16) and (18). Equation (16), that we repeat below for clarity,

$$\frac{dB}{dt} = (p_1^* - \mu_1^{(2)}(B))B),$$

describes a logistic-like growth. Moreover, the assumptions leading to equation (3) force p_1^* to be net rate of increase of the herbivore population which is made up of the difference between the emigration rate to leaves of highest quality and the quality dependent mortality rate; p_1^* being posistive, indicates the survival of the bugs depends in their ability to search and colonize leaves of the highest quality.

On the other hand, equation (18) can be rewritten as

$$\frac{dN}{dt} = (\gamma - \mu_0^{(2)}(N))N;$$

where $\gamma := k_{B^*}B^* + p_0^*$. Notice that the parameter $k_{B^*}B^*$ is related to the rate of usuccesful colonization of leaves. In this case, the total leaf population also has a logistic-type growth with γ being the expression for the net rate of increase. However in this case γ can be either positive or negative depending on the magnitud of p_0^*. If $\gamma > 0$ we have a growing population tending to an stable asymptotic equilibrium. This indicates that the proportion of

surviving leaves that are aphid-free because of unsuccesful colonizations outweights the proportion of leaves that die. If, however $\gamma < 0$, we obtain a unfeasible equilibrium point for the total leaf population. So, this model is valid only under the condition that γ is positive. If $\gamma > 0$ the quality distribution of leaves is given by formula (19) and it is independent of the total leaf density N. In conclusion one might say that the existence of a stable plant herbivore system within the setting of this model depends in the equilibrium between the ability of the herbivores to search and colonize leaves of the highest possible quality, and the ability of leaves of moderate qualities to avoid colonization and survive. Moreover, this model indicates that the total leaf and bug densities are independent of each other and that this type of hrbivore plant interaction affects only the quality distributions of leaves, and herbivores on leaves.

Equations (16) and (18) also indicate that density dependence in both populations affect only the growth rate of the total populations and has no effect on the quality profiles of neither one of both populations. Finally, it remains to asses the magnitud of our estimated parameters p_i^* by comparing them with published data. Further work needs to be done in this respect.

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Table 1. Observed and predicted values of the plant herbivore systems reported by Whitham(1978) who provided us with his original field data which constitute the observed portions of the table that follows; n^w, b^w are de experimental values of leaf and insect densities provided by Whitham(1978,1988), n^p, b^p are the predicted values of leaf and insect densities from equations (17) and (19).

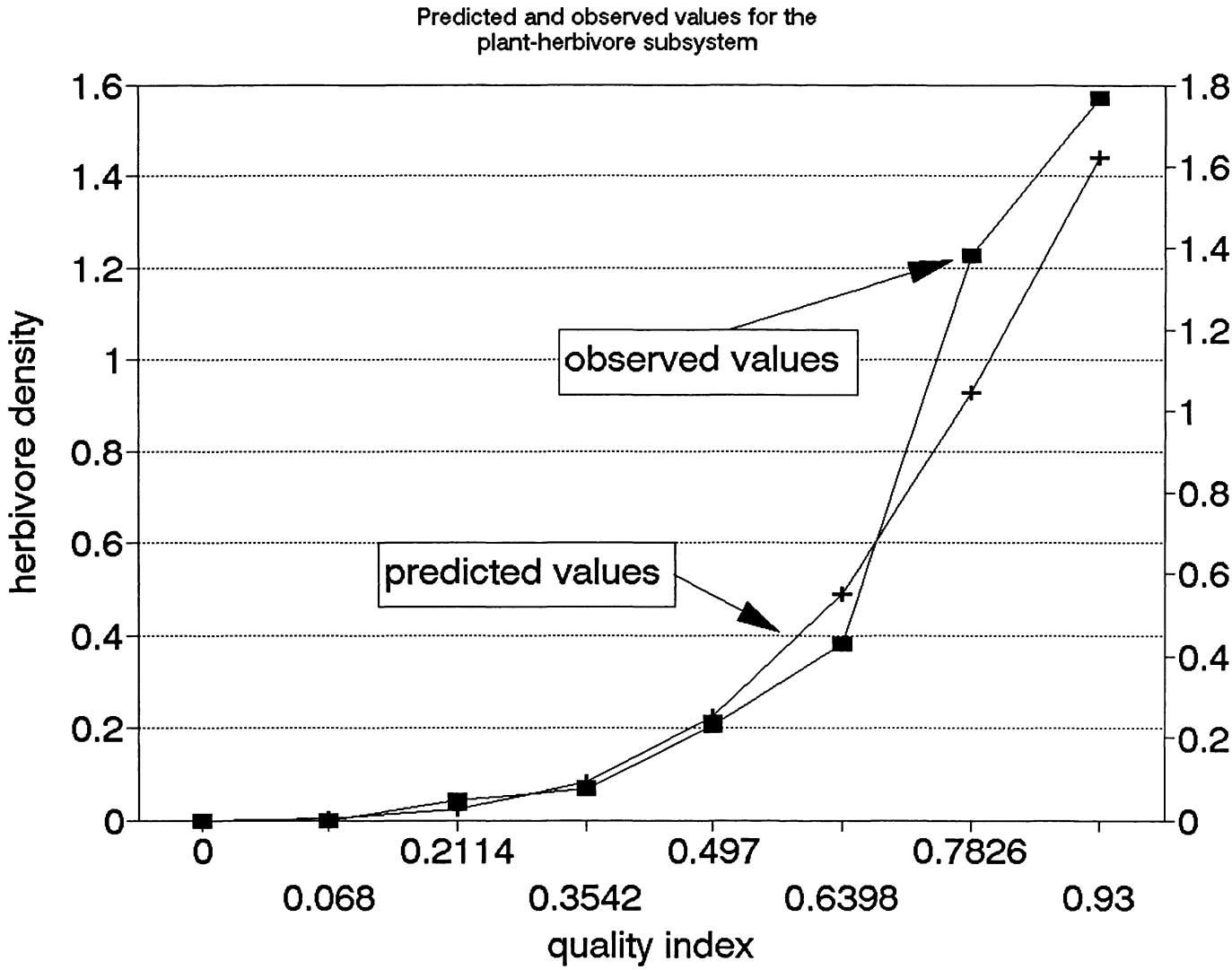
Plant susbsystem:

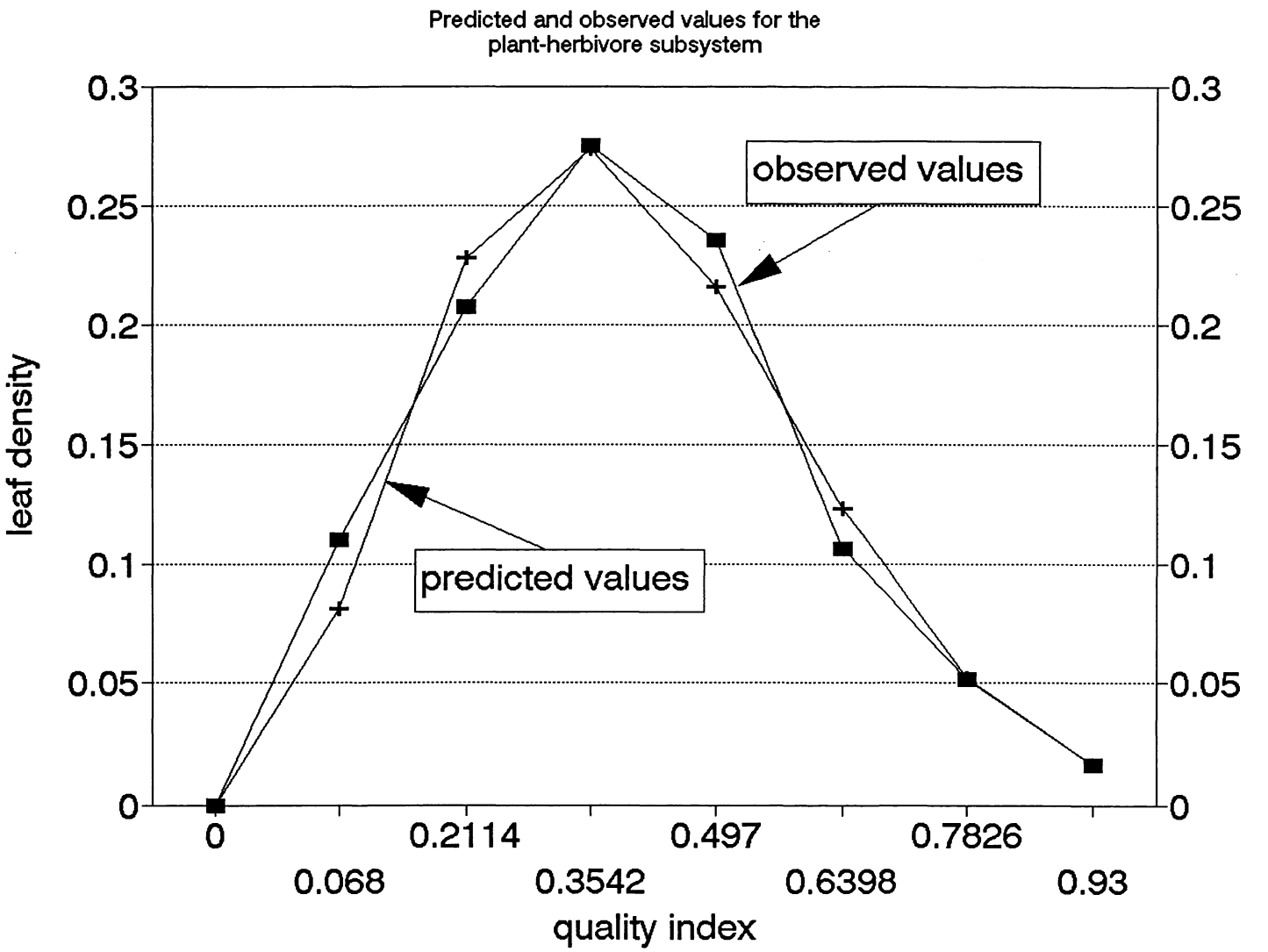
$$\mu_0 = 11.764018 \qquad p_0^* = -10.782822.$$

Herbivore subsystem:

$$\mu_1 = 6.041492 \qquad p_1^* = 1.142268.$$

quality index	n^w	n^p	residuals	b^w	b^p	residuals
0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.0688	0.1100	0.0813	0.0287	0.0000	0.0033	−.0033
0.2114	0.2070	0.2280	−.0210	0.0440	0.0252	0.0188
0.3542	0.2750	0.2733	$1.7E-3$	0.0680	0.0922	−.0242
0.4970	0.2350	0.2158	0.0192	0.2050	0.2499	−.0499
0.6398	0.1060	0.1230	−.0170	0.3800	0.5494	−.1654
0.7826	0.0520	0.0524	$-4.E-4$	1.2270	1.0450	0.1820
0.9300	0.0160	0.0163	$-3.E-4$	1.5710	1.6206	0.0496


Predicted and observed values for the plant-herbivore subsystem
herbivore density
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
observed values
predicted values
0
0.068
0.2114
0.3542
0.497
0.6398
0.7826
0.93
quality index


Predicted and observed values for the plant-herbivore subsystem
0.3
0.25
0.2
0.15
0.1
0.05
0
leaf density
observed values
predicted values
0
0.2114
0.497
0.7826
0.068
0.3542
0.6398
0.93
quality index